Finding good food and avoiding bad food: does it help to associate with experienced flockmates?

MICHAEL L. AVERY

U.S. Department of Agriculture, Denver Wildlife Research Center, Florida Field Station, 2820 E. University Avenue, Gainesville, FL 32601, U.S.A.

Abstract. Flocks of male red-winged blackbirds, *Agelaius phoeniceus*, were observed as they foraged on 9×12-m tilled plots within a 0·2-ha flight pen. One of the plots contained rice seed treated with the bird repellent methiocarb; a second plot received untreated rice. When each flock displayed a consistent avoidance of the treated plot, the number of experienced birds in the 12-bird flock was sequentially reduced to six, three, one and zero. Latency to use of the untreated plot and time spent foraging in the treated plot by naive birds were greatly reduced when at least one experienced bird was present. Throughout the 4-day trials, use of the treated seed plot by naive birds was greater than that of experienced birds. The naive flock members benefited by following experienced birds to the untreated seed plot, thereby discovering and using it more quickly than when no experienced birds were present. The naive birds did not avoid the treated seed plot, however, and many ate the treated seed and became sick. Thus, the benefit of associating with experienced birds was in learning where to forage, not where to avoid.

Birds foraging in flocks benefit over solitary foragers, primarily by reducing the per caput search time and the risk of predation (e.g. Pulliam & Millikan 1982). Furthermore, inexperienced or unsuccessful foragers may benefit by following successful individuals from a roost to a feeding site (e.g. Ward & Zahavi 1973).

Nevertheless, there are potential disadvantages for both experienced and inexperienced individuals feeding in flocks. Inexperienced birds feeding on an inappropriate food source or in an inappropriate location may influence, through social facilitation, the experienced flockmates to join them. Klopfer (1959) showed that greenfinches, *Chloris chloris*, 'could be made to ignore a discrimination which they had previously learned by observing wrong responses by an untrained individual'. Also, Turner (1964) showed that chaffinches, *Fringilla coelebs*, and house sparrows, *Passer domesticus*, would eat artificial food they normally avoided and feed in parts of the cage not normally used if they saw birds in adjoining cages doing so. Inexperienced birds that cue on the behaviour of experienced flockmates may not learn the independent cues needed to find food efficiently on their own (Beauchamp & Kacelnik 1991).

Red-winged blackbirds, *Agelaius phoeniceus*, commonly feed in flocks, and their feeding behaviour can be influenced by observing conspecifics (Mason & Reidinger 1981). It has also been shown that red-winged blackbirds can learn to avoid unpalatable food items (Rogers 1974), that food avoidance behaviour can be acquired through observational learning (Mason & Reidinger 1982), and that learned food aversions are more resistant to extinction than are learned food preferences (Mason et al. 1984).

Although red-winged blackbirds are flock-foragers, most experimental tests of food-avoidance learning in this species have focused on individuals or pairs (e.g. Rogers 1974; Mason & Reidinger 1982). The foraging behaviour of individuals or pairs may not accurately reflect behaviour in flocks because, in the field, red-winged blackbird flocks often consist of resident (experienced) and transient (inexperienced) components (Brugger et al. 1992). Under natural conditions, it is difficult to determine the extent and the nature of the interactions between these components of the foraging flock, so in this study I investigated the behaviour of experienced and inexperienced birds foraging in flocks under controlled conditions. Specifically, I asked the following questions.

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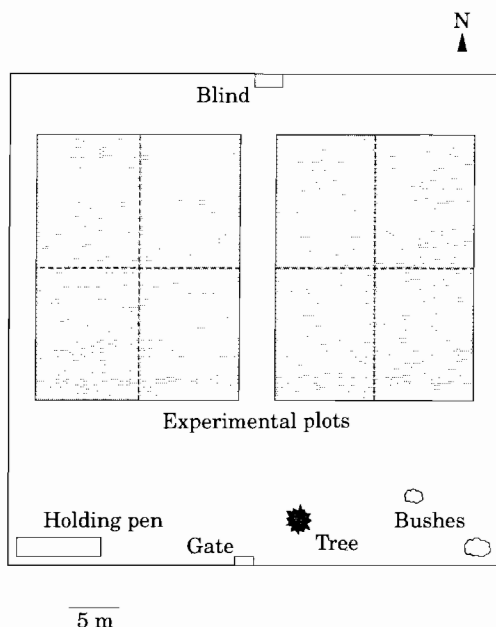
Figure 1. Locations of experimental feeding plots, the observation blind and the holding pen within the 0·2-ha flight pen used in the study.

(1) Do naive red-winged blackbirds find a quality foraging site more quickly when experienced birds are present than when there are no experienced birds in the flock?

(2) Do naive individuals avoid eating potentially harmful food when members of the flock already experienced with that food are present?

(3) Do the actions of naive individuals feeding on potentially harmful food affect the learned aversions of their experienced flockmates?

METHODS

The study was conducted inside a large (46 × 46 m) flight pen at the Denver Wildlife Research Center's Florida Field Station. Within the flight pen, I subdivided each of two 20 × 25-m bare, tilled areas into four 9 × 12-m plots (Fig. 1). The rest of the ground in the flight pen was grass-covered, and there were several bushes and small trees in the southeast corner.

For each replicate, I seeded one 9 × 12-m plot with untreated rice seed and seeded a second plot with rice treated with methiocarb (Mesurol 75% Seed Starter, Mobay Corp., Kansas City, Missouri) at 0·125% g/g, a rate equivalent to that recommended for preventing blackbird damage (Holler et al. 1982). Rice seed on the surface readily distinguished the two seeded plots from the six without rice seed. Methiocarb is a rapidly reversible cholinesterase inhibitor, and birds that consume methiocarb exhibit a range of symptoms including vomiting, ataxia, and temporary immobilization. Owing to these post-ingestional effects, birds readily form conditioned aversions to methiocarb-treated food (Rogers 1978).

The study consisted of three replications, each of which was a series of five 4-day feeding trials employing 50 different birds. To start each replication, I selected 12 male red-winged blackbirds at random from the Field Station's captive population and transferred them to a shaded holding pen (9 × 2 × 2 m) within the flight pen. Males were used exclusively because sufficient numbers of females could not be trapped. In the holding pen, the birds had free access to water, maintenance food (Purina Layena, Purina Mills, St Louis, Missouri), and unhulled rice.

After allowing the birds to acclimatize for 3 days in the holding pen, I tested them according to a set daily schedule. At 0800 hours, I released the birds from the holding pen and observed them from a blind at the north end of the flight pen (Fig. 1). I recorded the locations of the birds within the flight pen at 1-min intervals for the next 60 min and during 0800–0900 hours on subsequent days. Between 1200 and 1400 hours, I opened a 1 × 1-m drop-through entrance in the top of the holding pen to allow the 12-bird flock to re-enter. At 1630 hours, I removed the birds' maintenance food bowl from the holding pen so that they would be moderately hungry when released into the flight pen at 0800 hours the next morning. When use of the untreated plot by the initial group of 12 birds remained at least five times that of the treated plot for 3 days, those birds were considered 'experienced'. At that time, I replaced six randomly selected birds in the original flock with new birds from the captive population. The altered flock, now consisting of six 'experienced' birds and six 'naive' birds, was kept in the holding pen for 3 days to acclimatize, and then tested according to the daily schedule for the next 4 days. I marked each experienced bird with a numbered plastic leg tag of one colour while the naive birds were given similar tags of another colour.

Table I. Mean latency to use of the untreated plot and initial plot choice (treated or untreated) on the first day of feeding trials by red-winged blackbird flocks having varying numbers of experienced birds

Ratio of experienced: inexperienced birds per flock	Latency (s) to use of untreated plot and initial plot choice		
	Group 1	Group 2	Group 3
0:12	3600 (T)	3660 (T)	3600 (T)
1:11	1530 (U)	18 (U)	90 (U)
3:9	570 (U)	2580 (T)	870 (U)
6:6	150 (U)	160 (U)	100 (U)

T: Treated plot; U: untreated plot.

Next, I removed three of the original 'experienced' birds and all six of the 'naive' birds from the flock and replaced them with nine new birds selected at random from the captive population. After acclimation in the holding pen, this altered flock (3 'experienced', 9 'naive') was allowed to forage in the flight pen on the next four mornings. Then, I replaced 11 birds in this flock and tested the new altered flock, consisting of one 'experienced' bird and 11 'naive' ones. Finally, I replaced all 12 birds and recorded the behaviour of the all-naive flock. I repeated the entire procedure twice for a total of three replications, during each of which the ratio of experienced birds to naive birds in the 12-bird foraging flock progressively declined (12:0, 6:6, 3:9, 1:11, 0:12).

I evaluated flock performance by examining the initial choice of plot and the latency to use of the untreated plot. I analysed the number of min/bird recorded in the treated plot by naive and experienced components of mixed flocks in a three-way analysis of variance with repeated measures over days. In two replications, I monitored daily seed removal from the treated and untreated plots. Ten 0.19-m^2 sampling quadrats were located randomly within each plot and provisioned initially with 50 seeds each. Numbers of seeds taken during the 4-day trials were compared between groups and between plots in a two-way analysis of variance.

RESULTS

Initial Choice of Plot

In eight of the nine flocks with at least one experienced bird, the initial foraging site on day 1 was the untreated rice plot (Table I). The ninth

flock chose the untreated plot first on day 2. Without exception, experienced birds were the first to land in the untreated rice plot on day 1 of each flock's trial. In contrast, the flocks with no experienced birds did not locate the untreated plot during the initial 60-min period (Table I). These flocks each chose the untreated plot first on day 3 of their 4-day trials.

Use of the Treated Plot

Use of the treated plot by all-naive flocks greatly exceeded that of naive birds in mixed flocks (Fig. 2). Furthermore, use of the treated plot in mixed flocks was not affected ($F_{2,6}=0.02$, $P=0.979$) by flock composition. Overall, naive birds used the treated plot more than twice as much (0.79 min/bird versus 0.34 min/bird) as their experienced flockmates ($F_{1,6}=6.31$, $P=0.046$). This pattern of differential use did not vary ($F_{2,6}=0.60$, $P=0.578$) with the number of experienced birds in the flock.

Use of the treated plot on day 1 of a trial was greater ($F_{3,18}=5.05$, $P=0.010$) than on subsequent days (Fig. 3). The lack of an interaction with day ($F_{3,18}=0.68$, $P=0.575$) indicated that use of the treated plot by naive birds exceeded that by the experienced birds on all 4 days (Fig. 3).

Of the 5 days during which use of the treated plot by experienced birds exceeded 1 min/bird, 4 of the days were the first day of that flock's trial.

Replicate 2

Day 1 of 6:6. Initially, the entire flock foraged in the untreated plot for several min, after which birds began to explore other areas. Fourteen
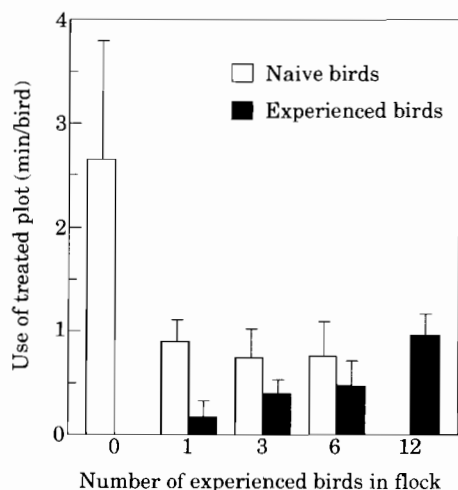
Figure 2. Use by experienced and naive red-winged blackbirds of a 9 × 12-m experimental plot sown with methiocarb-treated rice seed. The 12-bird experimental flocks were composed of varying numbers of experienced and naive individuals. Capped vertical bars indicate one standard error.
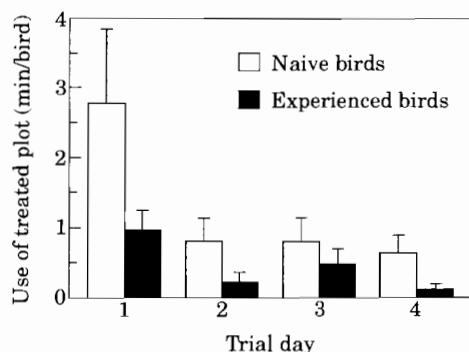
Figure 3. Use of the 9 × 12-m experimental plot sown with methiocarb-treated rice seed during 4-day feeding trials by experienced and naive red-winged blackbird flocks. Capped vertical bars indicate one standard error.

minutes into the trial, one naive and one experienced bird entered the treated plot and stayed for over 2 min. The naive bird ate several rice seeds, the experienced bird ate none. Within 5 min, the naive bird vomited beside the treated plot. After 33 min, three other naive birds entered the treated plot and two experienced birds followed. While the naive birds ate rice seed, the experienced birds probed under dirt clods and sticks for prey and also scavenged bits of broken rice seed dropped by

the naive birds. This type of scavenging behaviour, which continued for approximately 9 min, was not observed again. I saw no signs of illness.

Day 1 of 3:9. This flock began by feeding on the treated plot, with one of the experienced birds (G2) joined by the nine naive birds. The other experienced birds stayed out of the plot. Most birds left the plot within 3 min; then, 2 min later, I saw two of the naive birds vomit just outside the plot.

Day 3 of 3:9. The initial feeding site was the untreated plot and the flock stayed on the plot for 7 min. Then, one experienced bird (G5) and eight naive birds moved to the treated plot where they stayed for 4 min. It was not possible to determine which bird initiated the move to the treated plot, but once there, all appeared to feed on rice seed. After leaving the plot, several birds vomited and others perched quietly nearby.

Replicate 3

Day 1 of 6:6. Initially, experienced birds led the flock to the untreated plot where the flock fed for 2 min. Six minutes later, two experienced and one naive bird landed near the treated plot and walked into it, followed soon by the rest of the flock. The birds fed there for more than 2 min; then, 7–8 min later, four or five birds vomited and others appeared lethargic.

Day 1 of 1:11. After initially following the experienced bird and feeding for 2 min in the untreated plot, the group followed one of the naive birds to the treated plot where the flock foraged for 2 min more. No overt signs of illness were recorded.

Seed Removal from Test Plots

Estimated seed loss from the treated plot (0·7–2·3%; Table II) was less ($F_{1,8}=56·17$, $P<0·001$) than that from the untreated plot (35·6–58·7%). Seed loss was not affected ($F_{3,8}=1·00$, $P=0·44$) by group composition.

Evidence of Methiocarb Intoxication

On 13 of the 60 trial days, birds displayed signs of methiocarb intoxication after foraging in the

Table II. Numbers of seeds removed from plots with repellent-treated and untreated rice during 4-day feeding trials involving flocks of red-winged blackbirds with varying numbers of experienced birds

Ratio of experienced: inexperienced birds per flock	Number of rice seeds removed			
	Treated plot		Untreated plot	
	Group 2	Group 3	Group 2	Group 3
0:12	3	4	150	242
1:11	11	12	273	95
3:9	16	0	338	249
6:6	6	2	182	174

treated rice plot. Of the 10 times when vomiting occurred, seven were on the initial test day for that flock. Vomiting was also noted on test days 2 and 3 for one flock of 11 naive birds and one experienced bird, and on day 3 for one flock of nine naive and three experienced birds. Although I looked for it, I did not observe vomiting by an experienced bird. It was not possible to keep all birds in sight all of the time, however. Vomiting occurred as soon as 105 s and as late as 17 min after initial contact with the treated seed. One bird remained inactive for 55 min, but most affected birds resumed activity within 30 min of the initial reaction. All birds recovered completely from the temporary effects of the methiocarb-treated seeds.

DISCUSSION

Benefits of Associating with Experienced Birds

In this study, the value to the naive birds of associating with experienced birds was the more rapid location of the palatable rice seed. Nevertheless, even though the naive birds matched their experienced flockmates' behaviour by feeding in the untreated plot, they still spent more time in the treated seed plot than did the experienced birds. There are several possible reasons for this. The birds may have used the plot to forage on prey other than rice seed, or visits to the treated seed plot by naive birds may have occurred as they explored and learned about their new environment. Owing to the delay between ingestion and effect, perhaps some birds may not have associated the post-ingestional illness with the treated plot. Thus, for these birds, more than one visit to the treated plot was needed to establish an

avoidance response. Also, some birds might not have been exposed to a sufficiently noxious dose during the first visit to the treated seed plot and thus had no reason to avoid it.

For the naive blackbirds, the important factor was the presence or absence of experienced birds (Table I, Fig. 2), not how many were present. On the other hand, Chou & Richerson (1992) found that the ratio of demonstrators with a certain dietary preference did affect the food selection behaviour of untrained observer rats.

Blackbird flocks without at least one experienced member were disadvantaged by not readily locating the untreated plot and they averaged more time foraging on the treated seed. In the confinement of the flight pen, these disadvantages were not life-threatening. The naive birds soon became experienced and on their own eventually discovered and used the untreated plot. In nature, where finding a suitable feeding site is more problematic, survival may depend on associating with experienced birds and making use of their prior knowledge of feeding sites (Ward & Zahavi 1973).

Possible Negative Effects to Experienced Birds

It is not clear whether avoidance of methiocarb-treated seed by the experienced birds was affected by actions of naive birds. Some experienced flock members entered the treated plot and fed on rice; others foraged there without eating rice seed. Possibly, the strength of the aversion varied among individuals, and experienced birds that did feed on rice in the treated plot might not have been as well trained as those that did not.

Alternatively, the experienced birds could have been sampling their foraging environment (Krebs et al. 1978; Shettleworth 1984). Having been in the

holding pen for 3 days, the experienced birds might have visited the treated plot to re-acquaint themselves with the state of the food patch. Because birds can adjust their feeding behaviour to reduce exposure to dietary toxins (Hill 1972), sampling the treated seed plot probably entailed little risk to the experienced redwings. After confirming that the seed there was still unpalatable, their use again focused on the untreated plot.

Others (Klopfer 1959; Mason et al. 1984) have suggested that learned avoidance responses should be stable in opportunistic species, such as the red-winged blackbird. Definitive tests of this notion require detailed knowledge of individual responses which were not possible in this study. Nevertheless, the observed use of the treated seed plot and the taking of treated seed by some experienced birds suggest that an individual's learned avoidance response might be compromised in group feeding situations. Such attenuation, through subsequent social interactions, of individually acquired food aversions has been demonstrated in rats, *Rattus norvegicus* (Galef 1986), and spotted hyaenas, *Crocuta crocuta* (Yoerg 1991).

Avoiding Repellent-treated Seed

There were at least two ways that inexperienced birds could have avoided treated rice through interactions with flockmates. First, naive birds could have matched the behaviour of the experienced birds that fed in the untreated plot but did not visit the treated plot. This passive influence of the experienced birds did not, however, result in avoidance by the naive birds of the treated rice plot. The naive birds were shown where to feed, not where to avoid. In the absence of active intervention (e.g. Rothschild & Ford 1968) by experienced birds, the naive birds learned individually by trial and error the consequences of feeding in the treated rice plot.

Second, the untrained birds could have learned by direct observation of flockmates that had fed on the treated seed (Mason & Reidinger 1982). In almost every trial, some birds ate treated seed and became sick during the initial test day. Despite this, on subsequent days, birds still fed on the treated seed and became sick. The failure of the birds to learn by observing their flockmates' distress may have been due in part to affected birds moving from the treated plot prior to vomiting. Although some affected birds moved only 2–3 m off the plot, the lack of spatial contiguity may have made it difficult for unaffected birds to associate overt symptoms of methiocarb intoxication with the treated plot.

Repeatedly, it has been shown that rats do not acquire dietary aversions through observational learning (Galef 1985). Rats exhibit differential responses to ill and healthy conspecifics, but rather than avoiding food eaten by sick conspecifics, rats actually prefer such food (Galef et al. 1990). Thus, through social interaction, rats can learn which foods to eat, but not which to avoid (Galef 1985). Red-winged blackbirds in my study behaved like rats: social interaction enhanced their learning where to eat, but did not help the birds avoid repellent-treated food.

In contrast, previous investigations found that red-winged blackbirds can acquire robust dietary aversions through observational learning (Mason & Reidinger 1982; Mason et al. 1984). The absence of such behaviour by red-winged blackbirds in my study suggests that observational learning of food aversions is context-dependent. In the laboratory studies, prominent colour cues were paired with food eaten by ill conspecifics (Mason & Reidinger 1982; Mason et al. 1984). Singly caged observers subsequently avoided food paired with the appropriate colour. In the more natural setting of the flight pen, where flocks of red-winged blackbirds had only spatial cues available to them, no observational learning of dietary aversions occurred. Thus, learning that can occur in a laboratory environment might not be manifested under more complex social and environmental conditions.

Hierarchical Decisions in Feeding

Blackbirds and other flock-foraging species must make a series of decisions in their feeding behaviour (Sallabanks 1993). The results of my study suggest that information transfer through social interactions within the flock affects foraging decisions at some levels but not at others. Initially, birds must decide where to search for food. Birds making such coarse-level decisions can find food more quickly by following experienced, knowledgeable roostmates (Ward & Zahavi 1973; Pöysä 1992). In the flight pen, this meant locating the untreated 9×12-m plot quickly. Once at the

feeding site, however, the naive birds learned to avoid rice in the treated plot through individual trial and error. There was no evidence that naive birds altered their behaviour or rejected treated rice seed after observing adverse effects to their flockmates.

The latter result is perhaps not surprising, despite previous demonstrations of observational learning in laboratory studies (Mason & Reidinger 1982; Mason et al. 1984). Except when they are nesting, red-winged blackbirds primarily feed in flocks, and the diet of the birds during the non-nesting season is mainly seed and grain (Meanley 1971; Dolbeer et al. 1978). Because common grass, weed and crop seeds are not toxic, it seems unlikely that, while feeding in a flock, a red-winged blackbird will be exposed to toxins. In such situations then, selection for avoidance of toxic food items through social learning will not be great (Galef 1985).

On the other hand, an individual bird's ability to locate a suitable feeding site in an unfamiliar and changing landscape could be severely compromised without access to the knowledge of experienced birds. It is at this level, in environments that are spatially heterogeneous and temporally variable, that social transmission of information will be of greatest value to the individual red-winged blackbird, and behaviour enhancing the transmission of such knowledge will be favoured (Boyd & Richerson 1985).

ACKNOWLEDGMENTS

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